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Review

Endophyte symbiosis with tall fescue: how strong are the impacts on communities and ecosystems?

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ABSTRACT

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We have investigated community and ecosystem consequences of endophyte symbiosis with tall fescue over the past 13 y. *Lolium arundinaceum* is the most abundant plant in the eastern USA, and most is infected by the wild-type KY-31 endophyte *Neotyphodium coenophialum*. We established two large experimental grasslands (in 1994 and in 2000) with endophyte-infected or endophyte-free seed sown on recently plowed herbaceous vegetation. Other plant species established by seed or vegetative fragments. No other treatments were applied and plots were subject to natural biotic and abiotic variation. A third experiment examined ecological influences on endophyte infection dynamics starting from an intermediate infection frequency. Finally, we synthesized recent literature investigating the impacts of the tall fescue endophyte on the abundance of associated arthropod species. We found wide-ranging consequences of the endophyte from significant effects on soil feedback and decomposition rates, to plant-plant competition, diversity, productivity, invasibility and succession, to plant-herbivore interactions and energy flow through the food web. Further, we found that herbivore pressure caused rapid increases in infection frequency. Our results suggest that endophyte symbiosis in tall fescue can have a transforming effect on ecological systems.

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1. Introduction

Of all the systemic endophytes known in grass hosts, *Neotyphodium coenophialum* in tall fescue grass has received the most attention, in part due to the dominance of tall fescue in ecological systems worldwide. A great deal of work by many researchers has been conducted to unravel the evolutionary and genetic history of the tall fescue-endophyte association (Tsai *et al.* 1994; Craven *et al.* 2001a, b; Clay & Schardl 2002; Moon *et al.* 2004), to understand the effect of endophyte infection on the host plant (De Battista *et al.* 1990; Rice *et al.*

1990; West 1994; Malinowski & Belesky 2000; Newman *et al.* 2003), and to elucidate the underlying alkaloid biochemistry and impacts on animal consumers (Clay & Cheplick 1989; Hill *et al.* 1991; Agee & Hill 1994; Bush *et al.* 1997; Panaccione *et al.* 2001; Popay & Bonos 2005). Recent efforts have used the tools of molecular biology to create engineered endophyte strains with blocked pathways for alkaloid production (Panaccione *et al.* 2001; Young *et al.* 2005). In parallel, natural endophyte variants with different alkaloid production profiles have been incorporated into commercial germplasm (Bouton *et al.* 2002; Timper *et al.* 2005). Much research effort has also

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been devoted to similar questions with perennial ryegrass (*Lolium perenne*), meadow fescue (*L. pratense*) and annual ryegrass (*L. multiflorum*), as well as other grasses of economic importance (Wilson et al. 1991; White et al. 1992; Bazely et al. 1997; Cheplick & Cho 2003; Cheplick 2004a, b). New information about endophytes continues to accumulate, showing that endophyte alkaloids may enter the environment in unsuspected ways (Franzluebbers & Hill 2005; Koulman et al. 2007), and revealing that seed-transmitted, alkaloid-producing clavicipitaceous endophytes may also occur outside of monocotyledonous plants (Kucht et al. 2004).

Independent of the dominant grasses of managed forage and turfgrass systems worldwide, there has been much effort to quantify the diversity and frequency of endophyte-infected grasses in natural systems (Clay & Leuchtman 1989; Leuchtman 1992; Miles et al. 1998; Saikkonen et al. 2000; Moon et al. 2002; Zabalgoeazcoa et al. 2003; Faeth et al. 2006; Wei et al. 2006). However, relative to agronomic systems, many fewer studies in natural systems have examined experimentally how endophyte-infection affects plant performance and interspecific interactions (Pan & Clay 2002, 2003; Faeth & Sullivan 2003; Faeth et al. 2004; Tintjer & Rudgers 2006). While these grasses have been of little applied interest because endophyte-infection is often not vertically-transmitted through seeds, they represent a major component of the diversity of endophytes, of grasses, and of grass/endophyte interactions. With the growing interest in perennial grasses for biofuel production (Tilman et al. 2006), the improved biomass production conferred by endophytes in grasses may be of interest across a wider range of host taxa, regardless of the potential for disruption of grass sexual reproduction by stroma production.

Despite the diversity of past research and work in other systems, tall fescue remains the primary focus of research and the model system for grass-endophyte research. Arguably, most grass endophyte interactions worldwide are between tall fescue and *Neotyphodium coenophialum*. Tall fescue covers a significant area of the eastern USA, and is increasingly prevalent in South America, Australia, New Zealand, China and Africa. In the lower Midwest region of the USA, most tall fescue occurs on poor soils and is either unmanaged or lightly managed by occasional mowing. Much of this tall fescue was originally planted in the 1950's and 1960's, and has persisted *in situ* or spread locally from original plantings. Most of it is infected by the endophyte found in the tall fescue variety KY-31. Local collections in Indiana revealed no genetic diversity and the ubiquitous distribution of this single endophyte genotype (Leuchtman & Clay 1990).

Over the past 13 y we have investigated the community and ecosystem consequences of endophyte symbiosis with tall fescue (*Lolium arundinaceum*) in a series of long-term and large-scale field experiments in the lower Midwest, USA. The results of our studies do not bear directly on highly managed agricultural or turf systems, on tall fescue in other regions, or on other endophyte-infected grass species. However, they are relevant to the primary tall fescue zone in the lower Midwest and upper Southeast of the USA (Ball et al. 1993). In total, our research indicates that the endophyte of tall fescue is a keystone species with significant direct and indirect effects on community composition, trophic interactions and ecosystem

processes. The integrated and cumulative effect of endophyte symbiosis in tall fescue was far greater than individual taxon-focused studies would suggest. Our experimental results were highly consistent across plant communities that were geographically proximal but that differed in species composition, land use history, soil type and topography, suggesting that the effects of the endophyte symbiosis are robust and predictable. Moreover, they provide a baseline against which other studies and species can be compared.

Here, we provide an overview of the major results of our studies investigating the effects of endophyte infection of tall fescue on interspecific interactions, community composition and diversity, and ecosystem processes, such as primary productivity and decomposition. Our null hypothesis is that endophyte infection has no effect on community and ecosystem properties. In addition, we compare our results to those of other relevant studies through a synthesis of recent literature on the consequences of the tall fescue endophyte for arthropod communities. We use this synthesis to highlight new directions for future research.

2. Methods

Field experiment: documenting endophyte effects on the community

We established two large experimental grasslands (one in 1994 and one in 2000) where endophyte-infected (E+) or free (E-) seed (KY-31) was sown on recently plowed herbaceous vegetation. Plot sizes were either 20 m × 20 m (N = 8, upland site, 1994) or 30 m × 30 m (N = 16, lowland site, 2000). Details of these sites and local conditions are described in Clay & Holah (1999) and in Rudgers et al. (2007). Many other plant species established from the seed bank, dispersal or vegetative fragments. Both sites were also colonized by a diverse assemblage of invertebrate and vertebrate animals. Voles (*Microtus* spp.) were the dominant vertebrate grazer at both sites.

A series of measurements were typically taken twice per year, early in the growing season and then again late in the growing season. Vegetation was sampled by harvesting replicated quadrats (0.5 m × 0.5 m) randomly distributed across the plots. All above-ground vegetation was collected, sorted by species or into functional groups (tall fescue, other grasses, forbs and litter), and then dried and weighed. These data provided information on plant diversity, dominance, productivity and successional patterns (Clay & Holah 1999; Matthews & Clay 2001; Rudgers et al. 2004). In addition, all woody plants were comprehensively censused on an approximately annual basis, identified to species and measured for size (Rudgers et al. 2007). Voles were sampled by live-trapping and by radio collars (Fortier et al. 2000, 2001; Rudgers et al. 2007). Herbivorous arthropods were sampled by repeated sweep netting and pitfall trapping (Rudgers, unpublished). Spiders were sampled by exhaustive searching through litter in confined subplots, and by quantifying individual webs (Finkes et al. 2006). Alteration of soil properties following growth of E+ vs. E- tall fescue was quantified by taking soil cores from quadrats immediately following vegetation harvests, and then

growing three test species in individual soil cores from defined locations (Matthews & Clay 2001).

Field experiment: understanding ecological factors affecting endophyte frequency

Separate from these experiments where plots were either sown with 100% endophyte-infected or uninfected seed, an independent experiment was designed to examine the factors that might cause infection frequency to increase or decrease in mixed populations of tall fescue. A total of sixty 5 m × 5 m plots were established in the same general area as the 2000 experiment described above (Clay et al. 2005). All plots were sown with a 50:50 mixture of E+ and E- seed. Half of the plots were fenced to prevent entry by vertebrate herbivores and half of the plots were sprayed with a general contact insecticide (Malathion) to reduce insect herbivory. The two treatments were alternated with unfenced and unsprayed controls in a 2 × 2 design. We occasionally put live traps into fenced plots to remove renegade voles. The frequency of infection in the fescue population was sampled twice per year for five years using the tissue-print immunoblot procedure (Gwinn et al. 1991; Hiatt et al. 1999, 2001; Hill et al. 2002). Plots were kindly developed in Chris Schardl's lab at the University of Kentucky. Vegetation was sampled at the end of the study when four 0.5 m × 0.5 m quadrats were harvested per plot and separated into four components: tall fescue, other grasses, forbs or litter.

Literature synthesis: how tall fescue-Neotyphodium symbiosis may affect terrestrial food webs

We also synthesized research conducted during the past 10 y on how the endophyte in tall fescue may affect associated arthropods. We included only those studies that explicitly manipulated the presence (or type) of endophyte in tall fescue and examined effects on other species. We focused exclusively on experimental studies because, while naturally occurring infected and uninfected plants may show differences, effects of the endophyte cannot be separated from characteristics of the plant that may influence the probability or history of endophyte infection. In addition, we concentrated on studies of wild animals rather than domesticated species. We also included endophyte-mediated influences on fitness related variables and the performance of animals rather than on behaviors or preferences because these effects will likely have more direct effects on species distributions and abundances. For each study (Appendix 1), we determined the magnitude of the effect of the endophyte treatment, quantified here as the log response ratio $L = \ln(\text{mean}_{\text{endophyte-free}} / \text{mean}_{\text{endophyte}})$ (Hedges et al. 1999) to allow for scale-independent, cross-study comparisons of the strength of the endophyte's influence.

3. Results and discussion

Plant diversity and productivity

Twice-yearly sampling of vegetation in the upland plots established in 1994 revealed that endophyte infection of tall fescue

led to the competitive dominance of the host and suppression of other plant species (Clay & Holah 1999). Endophyte-free (E-) plots has less tall fescue, greater biomass of other perennial grasses and more forbs compared to endophyte-infected (E+) plots (Fig 1). Of special note was the nearly complete loss of forbs from E+ plots after four years (Clay & Holah 1999). There was no effect of endophyte infection on total productivity, but a strong effect on the proportional contribution of different groups to total plant biomass. In parallel, plant species richness steadily declined in plots with the endophyte. The design of the study allowed us to attribute changes in response variables to either endophyte infection or random environmental variation among plots. For both species richness and composition of biomass, there was no effect of endophyte infection during the first two years of the study and all of the variation occurred between plots within a treatment. However, after four years endophyte infection explained nearly 50% of the variation in response variables while plot explained very little. Thus, endophyte presence ultimately overwhelmed environmental variation in explaining plant composition.

We hypothesize that the primary mechanism driving changes in vegetation between E+ and E- plots was differential herbivory, primarily by voles (see additional evidence below). We suggest that voles consumed tall fescue in the E- plots, alleviating grazing pressure on other plant species (grasses, forbs, tree seedlings). In contrast, in E+ plots voles avoided E+ fescue, preferentially consuming other plants species including tree seedlings (Rudgers et al. 2007). Thus, declines in plant diversity were mediated indirectly through

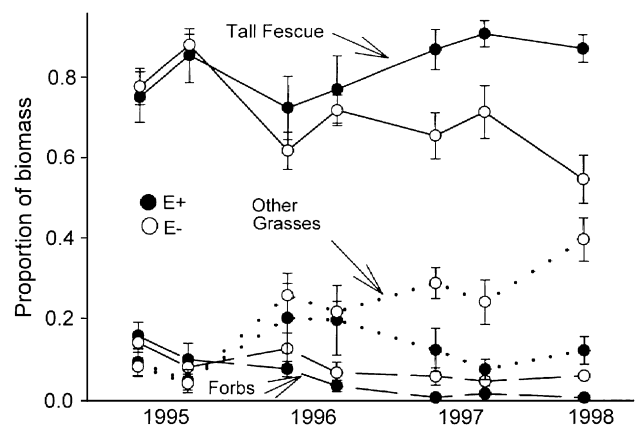


Fig. 1 – Changes in biomass composition. We divided total standing biomass into three proportions: tall fescue, other grasses, and forbs. Both the proportion of tall fescue and proportion of grasses other than fescue changed linearly over time depending on the infection status of the plot ($F_{1,6} = 11.51$, $P = 0.015$; $F_{1,6} = 13.16$, $P = 0.011$ for fescue and other grasses, respectively). The proportion of forb species did not change linearly through time depending on infection status ($F_{1,6} = 4.41$; $P = 0.081$) but has significantly decreased generally through time ($F_{1,6} = 48.87$; $P = 0.0004$). Statistics are the results of repeated measures ANOVA using plot means and a first-degree polynomial contrast for time. Reprinted with permission from Clay & Holah (1999).

altered feeding behavior in the dominant vertebrate consumer.

Strong effects of the endophyte on plant diversity are likely to be scale-dependent. At the scale of our experiments (and the scale at which tall fescue is normally planted), we expect voles to have little choice about the presence of E+ fescue, because territory sizes are smaller than plot or field sizes (Fortier *et al.* 2001). If experiments were conducted on a smaller, less realistic scale, voles may be able to concentrate feeding in E- patch types and community-level responses may be less pronounced.

Finally, while voles appear to be a key driver in this system, other mechanisms may also contribute to the altered plant community. Allelopathy (Orr *et al.* 2005), alteration of decomposition rates and soil communities (Matthews & Clay 2001; Lemons *et al.* 2005), direct competition (Clay *et al.* 1993), and differential insect herbivory mediated by the endophyte's presence (Breen 1994) may play minor roles, and the relative importance of these mechanisms in altering the plant community remains to be determined. A few other studies have compared vegetation in contrasting areas with E+ or E- fescue but they have been uncontrolled, non-experimental or lacking in knowledge about starting conditions. There is a need for more field experiments of the types described here across a greater diversity of environmental conditions.

Plant succession

In both the upland and lowland experimental tall fescue grasslands, the presence of the endophyte suppressed the natural transition from grassland communities to forests (Rudgers *et al.* 2007). The endophyte reduced tree abundance by 60-80% across the two experimental sites. Endophyte symbiosis caused declines in the abundance and/or growth of silver maple, red osier dogwood, and white ash, but had no significant influence on the growth or abundance of white mulberry, which was only present at the upland site (1994 planting). Importantly, consumption of tree seedlings by voles (*Microtus* spp.) was 65% higher in plots with the endophyte at one (lowland) site where these data were collected (Fig 2). Vole predation on woody species appears to be more severe in E+ plots because the dominant plant (E+ tall fescue) was unpalatable to voles, and as a result, voles fed more heavily on other species. Finally, the endophyte in tall fescue had the overall effect of stabilizing plant community composition by significantly reducing temporal fluctuations in the presence of both woody and herbaceous plant species. Despite its negligible contribution to community biomass, the endophyte poses an important constraint on the natural transition from grasslands to forests in the Midwest.

Diversity – ecosystem functioning relationships

A large number of studies in community ecology during the past decade have investigated the impacts of biodiversity on ecosystem functioning (Hooper & Vitousek 1997; Tilman 1999). We examined how endophyte infection of tall fescue

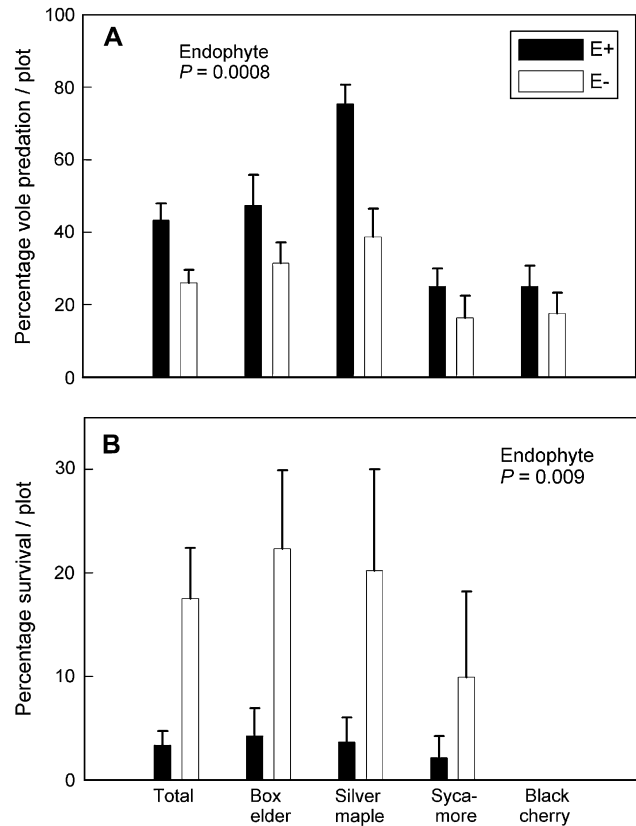


Fig. 2 – Fates of tree seedlings planted into lowland plots enriched with endophyte-infected (E+, filled bars) or endophyte-free (E-, open bars) tall fescue. (A) Mean percentage seedling predation by voles per plot (endophyte $F_{1,56} = 12.7$, $P = 0.0008$, $n = 8$ plots), and (B) mean percentage survival per plot after three months (endophyte $F_{1,42} = 7.5$, $P = 0.009$, $n = 8$ plots – black cherry not included in this analysis because no plants survived). With the exception of black cherry survival, the tree species responded similarly to the endophyte (endophyte \times species, predation $F_{3,56} = 1.3$, $P = 0.3$; survival $F_{2,42} = 0.8$, $P = 0.5$). Bars show means + s.e.m. Reprinted with permission from Rudgers *et al.* (2007).

modifies the relationship between diversity and both productivity and invisibility. Using a graphical model, we predicted that endophyte infection would weaken the predicted correlation between species diversity and ecosystem properties. We tested this model using field data from the 100% E+ and 100% E- field plots at the upland site, which supported a diverse array of other plant species (Rudgers *et al.* 2004). We also constructed a greenhouse experiment that experimentally varied the diversity of native prairie perennials in pots (Rudgers *et al.* 2005). Once prairie communities established, we added E+ or E- tall fescue as an invader. In both field and greenhouse studies, we found that endophyte infection in the invader weakened the negative relationship between plant species diversity and the establishment of the invader (Fig 3). These results demonstrate that the presence of an

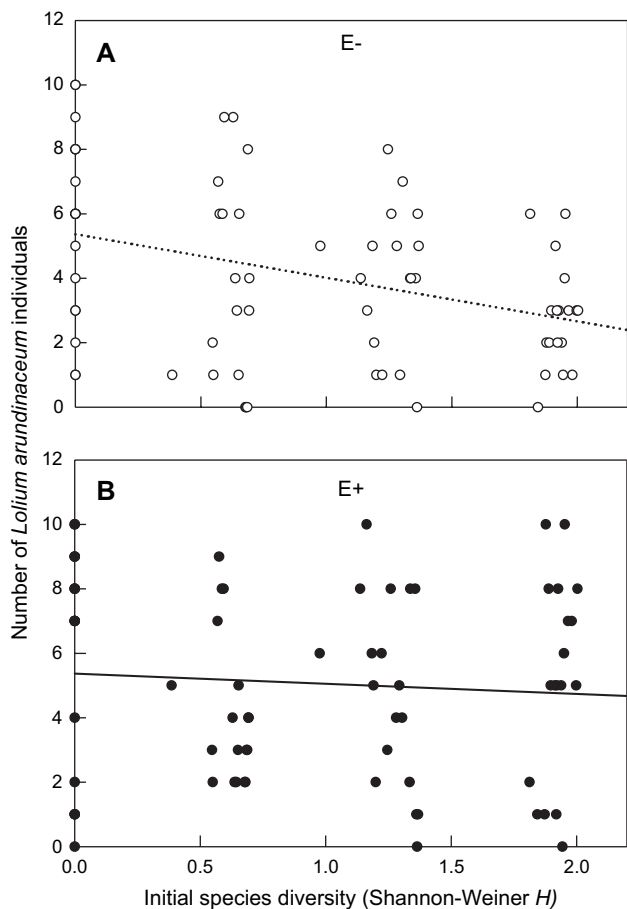


Fig. 3 – The number of surviving *Lolium arundinaceum* individuals by initial plant species diversity (A) without the endophyte, *Neotyphodium coenophialum* (E-) (regression: Number = $-1.35 \times$ initial diversity + 5.37, $r = -0.36$, $P = 0.0018$, $n = 72$) and (B) with the endophyte (E+) (regression: Number = $-0.31 \times$ initial diversity + 5.37, $r = -0.08$, $P = 0.53$, $n = 72$). Reprinted with permission from Rudgers et al. (2005).

endophyte in a dominant grass can modify biodiversity-ecosystem functioning relationships.

Soil and plant-soil feedbacks

Most prior research has focused on the above-ground environment of tall fescue and how the endophyte affects plant performance and interspecific interactions. Although the endophyte does not occur in roots, there may be indirect effects on below-ground properties and processes (Pedersen et al. 1988; Chu-chou et al. 1992; Grewal et al. 1995; Malinowski et al. 1998; Franzluebbers & Hill 2005). Here, to determine if the growth of E+ vs. E- fescue affects subsequent plant growth in the same soil, soil cores were removed from E+ or E- experimental plots following vegetation sampling, and then planted with E+ or E- tall fescue, *Plantago lanceolata* or *Trifolium repens*. The growth of those species was analyzed in relation to the past endophyte status of the plot and the composition of

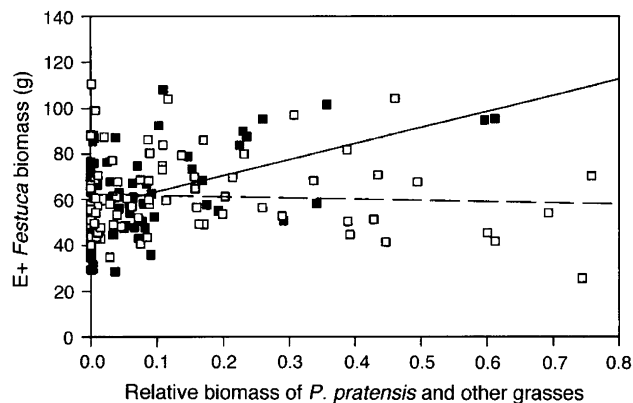


Fig. 4 – Regressions of experimental E+ *Lolium arundinaceum* total biomass on previous biomass of *Poa pratensis*, *Dactylis glomerata*, *Poa compressa*, *Bromus commutatus*, and *Agrostis alba*, relative to other plants species in soil from E+ plots (filled squares and solid line: $F_{1,78} = 21.37$, $P < 0.0001$, $r^2 = 0.22$) and in soil from E- plots (open squares and dashed line: $F_{1,78} = 0.17$, $P = 0.68$, $r^2 = 0.002$). Relative biomasses were proportions and were arcsine square-root transformed before analyses. Reprinted with permission from Matthews & Clay (2001).

the harvested above-ground vegetation. We found that the endophyte status of the plot from which cores were obtained had no direct effect on plant performance (Matthews & Clay 2001). However, experimental plant responses suggest that, by inducing changes in plant community composition, E+ fescue may indirectly affect soil properties. In particular, tall fescue biomass was lower when grown in soil previously dominated by E+ fescue compared to soil previously dominated by Kentucky bluegrass and quackgrass (Fig 4). This pattern indicates negative feedback (accumulation of detrimental organisms) on the growth of E+ fescue and represents a potential long-term constraint on E+ fescue's ecological dominance. Interestingly, the feedback was endophyte specific: no effect was seen on E- fescue or in soil previously dominated by E- fescue.

Another important soil process is decomposition of litter and other organic matter. In the lowland field experiment, we used reciprocal transplants of E+ and E- litter into E+ or E- plots (Lemons et al. 2005). After 10 m in the field, decomposition of the litter was significantly slower for E+ fescue litter than for E- litter (Fig 5). Decomposition also depended on a complex interaction between the litter source (collected from E+ or E- plots), the decomposition microenvironment (E+ or E- plots), and the presence of mesoinvertebrates (manipulated by the mesh size of litter bags). When mesoinvertebrates were excluded using fine mesh and litter was placed in a microenvironment with the endophyte, the difference between E+ and E- litter was strongest.

Several prior studies have further examined the how endophyte infection affects soil properties and processes. For example, Omacini et al. (2004) found that litter decomposition in microcosms using *Lolium multiflorum* was affected by

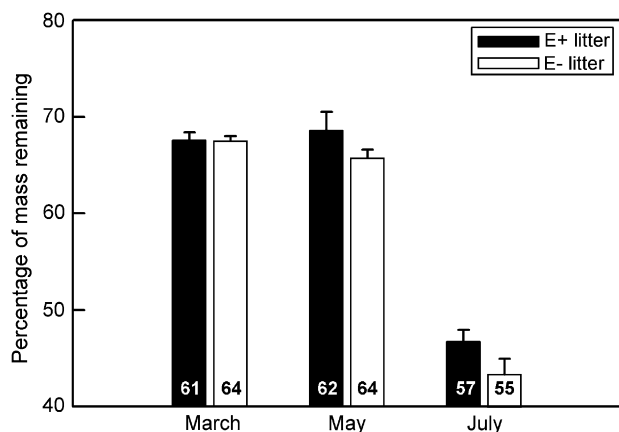


Fig. 5 – Effect of the endophyte (*Neotyphodium coenophialum*) treatment on the percentage remaining dry mass of litter from field plots of *Lolium arundinaceum* over three census dates. E+ = litter with the endophyte, E- = litter lacking the endophyte. Bars represent means with s.e. Sample sizes (number of litter bags) are given on each bar; unequal sample sizes resulted from some bags being lost or damaged in the field. Reprinted with permission from Lemons et al. (2005)

endophyte status. Similarly, Franzluebbers and colleagues have demonstrated significant changes in carbon and nitrogen pools as well as alkaloid levels in soils beneath E+ versus E- tall fescue (Franzluebbers et al. 1999; Franzluebbers & Hill 2005; Franzluebbers & Stuedemann 2005; Franzluebbers 2006). Other studies have documented changes in mycorrhizal and nematode communities with endophyte infection (West et al. 1988; Kimmons et al. 1990; Chu-chou et al. 1992; Omacini et al. 2006). All of these alterations could feed back to alter the performance of both tall fescue and neighboring plant species (Orr et al. 2005). At this stage, it remains unclear to what degree changes in soil properties and communities influence aboveground shifts in community composition. This area is ripe for further investigation.

Factors affecting infection dynamics in mixed populations

Our prior field experiments were conducted in plots with near 100% E+ or E- tall fescue. This design makes it easy to detect effects of the endophyte, and reflects the common all or nothing endophyte status of many populations of tall fescue (Clay 1997). However, many populations of endophyte-hosting grass species have intermediate levels of infection (Latch et al. 1987; Shelby & Dalrymple 1987; Saikkonen et al. 2000; Spyreas et al. 2001). The question arises whether intermediate infection frequencies are stable or change in a directional way towards complete infection or loss of infection. In the latter case, what ecological factors may drive infection frequency changes? We established replicated plots with tall fescue at initial 50% infection frequency and manipulated herbivore pressure by a combination of fencing and/or insecticide application with controls. Infection frequency

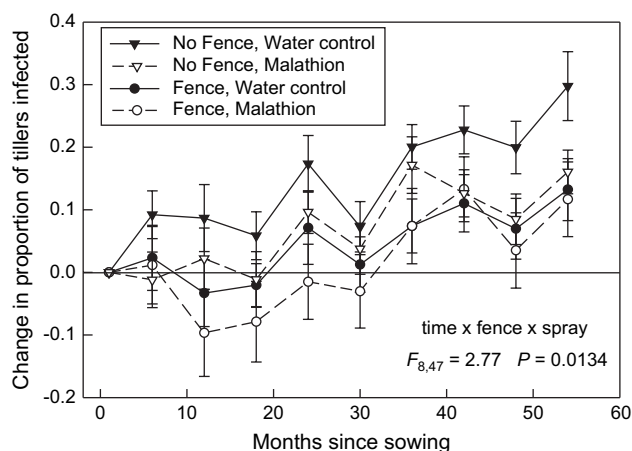


Fig. 6 – The change in endophyte frequency among treatments. The change in frequency was determined by subtracting the initial proportion of tillers infected in that plot from the proportion of tillers infected on each date. The change in proportion is bounded by 0.5 and -0.5 (0% and 100% infected, respectively). Over time, infection increased in all plots (time, $F_{8,47} = 29.6$, $P < 0.0001$). Treatments diverged over time (fence \times insecticide \times time interaction, $F_{8,47} = 2.8$, $P < 0.01$). No main effects or two-way interactions were significant (fence, $F_{1,54} = 3.1$, $P < 0.08$; fence \times time, $F_{8,47} = 1.4$, $P < 0.2$; insecticide, $F_{1,54} = 1.9$, $P < 0.2$; insecticide \times time, $F_{8,47} = 0.8$, $P < 0.6$; fence \times insecticide, $F_{1,54} = 0.43$, $P < 0.5$). Symbols show means \pm SE and are slightly offset to show error bars clearly. P values indicate a significant difference between the dual herbivore-exclusion treatment (fenced plus insecticide) and the control (unfenced plus water) for each date. Reprinted with permission from Clay et al. (2005).

rapidly increased from 50% to 80% over a five-year period in unfenced, unsprayed plots subject to the greatest herbivore pressure (Fig 6, Clay et al. 2005). In contrast, the smallest increase in infection frequency occurred in plots protected from both vertebrate and insect herbivory. These results revealed that herbivores select for highly infected tall fescue, at least under our experimental conditions, and strongly support the defensive mutualism hypothesis (Clay 1988). However, endophyte-infection frequency increased under all treatments indicating that other factors may also favor infected fescue (Fig 6). Alternatively, our treatments were not 100% effective and the uncontrolled herbivory may be responsible for the overall increase in infection frequency. In any case, these results emphasize that the tall fescue/endophyte relationship is highly mutualistic under normal circumstances in its introduced range (but see Cheplick et al. 1989).

Several other studies have tracked changes in infection frequency over time, but have generally not applied experimental treatments (Thompson et al. 1989; Shelby & Dalrymple 1993). In one notable case with perennial ryegrass (Francis & Baird 1989), Argentine stem weevil herbivory drove a rapid loss of uninfected ryegrass seedlings from populations. To

our knowledge, in all studies where infection frequency was monitored over time, endophyte infection frequency either increased or remained the same but never decreased in the same population. However, there have been relatively few studies of this type, and more are needed from a variety of species. In particular, could there be frequency dependence such that the relative fitness advantage of E+ fescue depends on the overall infection level in the population? Given that animals may be able to detoxify alkaloids up to a certain point, endophyte infection may provide no defense if its frequency is low, or the host is rare.

Literature synthesis: how endophyte symbiosis may affect terrestrial food webs

Aboveground herbivores and seed predators

The *Neotyphodium* endophyte in tall fescue can strongly reduce the abundances of individual herbivores. Insects adversely affected by endophytes are taxonomically diverse, including generalist as well as grass specialist species in the Lepidoptera, Orthoptera, Hemiptera, Diptera, and Coleoptera (reviewed by Latch 1993; Breen 1994; Clay 1996; Rudgers et al. 2005), see also species list in Clement et al. 1994). In our survey of the recent literature (Appendix 1), the strength of the endophyte effect differed among types of feeding guilds, with the strongest effects on leaf chewers and more moderate effects on sap (xylem and phloem) feeders. In addition, effect sizes were stronger for species characterized as grass specialists than for species known to consume a broader diet (generalists), perhaps resulting from the ability of generalists to dilute the toxic effects of fungal alkaloids with a more diverse diet. We found very weak effect sizes for the endophyte's influence on vertebrate seed predators (no recent invertebrate studies have been conducted), especially relative to endophyte effects on vertebrate leaf chewers (rabbits, mice, voles, etc.) (Appendix 1). However, surprisingly few total species have been investigated in detail given the wide range of organisms that co-occur with tall fescue, and most studies, not unexpectedly, have focused on important forage and turf pests.

Belowground herbivores and detritivores

Despite the localization of *Neotyphodium coenophialum* in aboveground tissues, root-feeding insects and detritivores can be inhibited by endophyte infection. For example, Elmi et al. (2000) found complete mortality of the root knot nematode (*Meloidogyne marylandi*) in pots of endophyte-infected, but not in uninfected tall fescue. Similarly, survival of Japanese beetle (*Popillia japonica*) larvae belowground was reduced in pots of highly infected tall fescue compared to pots containing lower infection levels (Oliver et al. 1990), although across field and lab studies, results for endophyte effects on Japanese beetles have been equivocal. Our review of current literature shows much smaller effect sizes for the endophyte on root feeders than any other herbivorous group excepting vertebrate seed predators. Weak effects on root feeders are not unexpected, given that the endophyte is localized in aboveground plant tissues.

In addition to changes in belowground herbivores, we (and others) have found plot-level changes in the detritivore assemblage. However, overall endophyte-mediated effects on detritivores were small (85 % smaller effect sizes) relative to effects on invertebrate herbivores. Previous plot level studies show declines in some detritivores, including Chloropid flies, oribatid mites, the collembolan species *Lepidocyrtus cinereus*, and in the reproductive output of earthworms (Bernard et al. 1997; Humphries et al. 2001). However, a few species appear to be unaffected or even enhanced by endophytes (e.g. earthworm abundance, Sminthurid collembola (Davidson & Potter 1995; Bernard et al. 1997), Hypogastruridae (Lemons et al. 2005)). In our work, the total abundance of one keystone detritivore group, the Collembola, did not significantly differ between endophyte treatments (E+ vs. E-), but the composition of collembolan families significantly diverged (Lemons et al. 2005), with Hypogastruridae abundance greater in E+ plots and Isotomidae abundance higher in E- plots. These results are consistent with other studies that demonstrate Hypogastruridae tolerate toxic environments (e.g., waste dumps and heavy metal sites) and Isotomidae are especially sensitive to environmental toxins (Fountain & Hopkin 2005). A broader examination of the decomposer food web is needed, and the mechanisms underlying shifts in detritivores due to the endophyte remain unresolved.

Predators and parasitoids

Endophytes, particularly through their effects on insect herbivores, can indirectly modify the abundance or composition of higher trophic levels. Indirect effects may occur through endophyte-mediated reductions in the quality or abundance of prey or through changes in prey behavior. Moving up through the food web, the effects of endophytes may remain similarly strong, accumulate, or attenuate. Most studies to date support attenuation of endophyte effects on arthropod predators and parasitoids, with an effect size of the endophyte that is 90 % smaller for predators and parasitoids relative to invertebrate herbivores. In comparison, multitrophic level effects seem stronger in related grass-endophyte systems (e.g., perennial ryegrass-Argentine stem weevil-parasitoid, Bultman et al. 1996, 1997), and Italian ryegrass-aphid-parasitoid interactions, (Omacini et al. 2001). However, surprisingly less attention has been given to multitrophic level interactions in the tall fescue system, given its ecological dominance, particularly in the USA.

The majority of studies testing for higher trophic level impacts of grass-endophyte interactions have examined parasitoids. Parasitoids typically have more specialized diets than predators of herbivores, and may be more sensitive to the presence of microbes in plants. For example, Omacini et al. (2001) found that infected *Lolium multiflorum* (Italian ryegrass) reduced the rate of parasitism of aphids by several parasitoid species.

Endophyte effects on generalist predators range from endophyte-mediated enhancement of predation to endophyte-mediated suppression. For example, entomopathogenic nematodes acted synergistically with the endophyte to reduce Japanese beetle (*Popillia japonica*) survival more

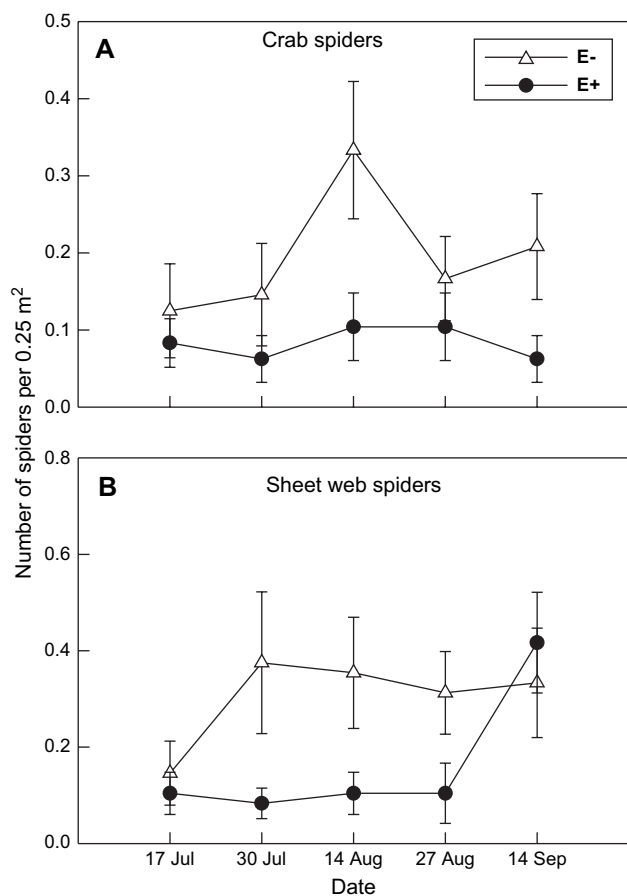


Fig 7 – Effect of manipulation of the presence of *Neotyphodium coenophialum* in *Lolium arundinaceum* on the density of spiders in the families (a) Crab spiders (Thomisidae) and (b) Sheet web spiders (Linyphiidae) surveyed in 30 m × 30 m field plots in Bloomington, Indiana. Data points represent the mean abundance of spiders, and the bars show ± 1 SE. For the endophyte, treatments are represented as endophyte-infected (E+ = solid circles) or endophyte-free (E- = open triangles), n = 8 plots per treatment. Reprinted with permission from Finkes et al. (2006).

than either factor alone (Grewal et al. 1995). In this case, fungal alkaloids appear responsible by reducing beetle consumption and mass and enhancing susceptibility to predation (Grewal et al. 1995). More recent work with Japanese beetles suggested a neutral effect of the endophyte on susceptibility to nematodes (Koppenhofer et al. 2003); thus, additional research is needed even for this well-studied species. Surveys of generalist arthropod predators in field plots suggest the ants, spiders (Araneae), and two beetle groups (Staphylinidae and Carabidae) may be insensitive to the presence of the endophyte (Bernard et al. 1997; Koppenhofer et al. 2003), at least when grouped at this broad taxonomic level. However, our work suggests that more attention to changes in composition within large taxonomic groups, such as order or family, is likely to reveal stronger endophyte effects. For example, while we found no effects of endophyte presence

on the total abundance of spiders, there were significant reductions in the abundance of two important families: the crab spiders (Thomisidae) and sheet web-weaving spiders (Linyphiidae) due to the presence of the endophyte (Finkes et al. 2006, Fig 7). At this stage, we can only speculate on mechanisms driving these effects, although prey capture rates were significantly lower for one common orb-weaving spider (Araneidae) in E+ versus E- tall fescue plots.

Arthropod community structure

Many studies have examined the effects of endophytes on individual herbivores, but few investigations have considered entire arthropod communities. In agronomic, as well as naturalized tall fescue ecosystems, identification of these broader community level impacts are important to improving pest control and conserving biodiversity. We predict, based on studies with individual herbivores, that the endophyte in tall fescue will reduce the overall abundance and species diversity of invertebrate herbivores. Reductions may occur directly through the deterrent action of fungal alkaloids and/or indirectly through reductions in plant diversity (bottom-up effect) or in the diversity of higher trophic levels (top-down effect). Most likely, for complex natural food webs, the endophyte will alter community structure through a multitude of direct and indirect pathways. To our knowledge, only three prior studies have experimentally tested for an effect of *Neotyphodium coenophialum* on the arthropod community as a whole; none surveyed comprehensively across taxa. Murphy et al. (1993) found fewer total turfgrass pests in plots of E+ tall fescue relative to E- plots. In a second study, endophyte symbiosis reduced two aphid species, two leafhoppers, a flea beetle, and Staphylinid beetles, but had minimal effects on mites, predaceous arthropods, earthworms, Japanese beetles and three other aphid species (Davidson & Potter 1995). Dissertation work by Willver (summarized in Bernard et al. 1997) found no effects of the endophyte on dipturans or Carabid beetles, but identified declines in some other detritivores (Appendix 1). Unfortunately, most of these studies focused on the abundance responses of particular taxonomic groups and did not characterize other changes in community structure, such as species richness, taxonomic diversity, evenness, or composition. In one exception, (Muegge et al. 1991) found significant declines in the species richness of two insect families (Cicadellidae and Cercopidae) in field plots with the endophyte (Appendix 1).

Capturing these more detailed changes in community structure has been a goal of current research by our groups, because of our interest, more broadly, in understanding how mutualisms influence the dynamics of communities. In general, results show that experimental elimination of the endophyte in tall fescue enhances the diversity of several guilds of arthropods, including herbivores, spiders and other predators, and increases the total abundance of insect herbivores (Rudgers & Clay 2005 and unpublished data). These patterns indicate that finer-scale investigations of non-herbivore species are likely to reveal stronger effects of the endophyte than thus far reported.

A role for endophyte genotype?

Endophyte genotypes differ in compatibility with grass genotypes (Leuchtman & Clay 1989a; Christensen *et al.* 1997), production of alkaloids (Siegel *et al.* 1990; Hill *et al.* 1991; Wilkinson *et al.* 2000; Leuchtman *et al.* 2000; Rasmussen *et al.* 2007), resistance to herbivores (Leuchtman *et al.* 2000; Timper *et al.* 2001, 2005; Tintjer & Rudgers 2006), production of stromata (Leuchtman & Clay 1989b), mycelial mass (Hiatt & Hill 1997), and effects on the phenotypic plasticity of grasses (Cheplick 1998). Endophyte genotypes that differ in the types and amounts of alkaloids they produce can have dramatically different effects on herbivores, particularly insects *versus* mammals. For example, endophyte genotypes have been introduced for forage grasses that lack the production of ergot alkaloids and consequently lack toxicity to livestock (Bouton *et al.* 2002). Similarly, the fungal alkaloid peramine affected one species of aphid, but combinations of both peramine and loline alkaloids were required for deterrence of other aphid species (Siegel *et al.* 1990; see also Hunt & Newman 2005).

In ongoing work, we are exploring the relative importance of plant *versus* endophyte genotype in affecting the diversity and abundance of other community members. Results thus far suggest that endophyte genotype does significantly alter plant and insect communities, but that these effects depend on the genetic background of tall fescue. Predicting how endophyte genotype alters community structure may ultimately depend on testing unique combinations of both host plant and microbe genotypes. Genetic modification of endophytes to eliminate the production of the mammalian toxin, ergovaline, has been accomplished (Panaccione *et al.* 2001), and directly incorporating genes from endophytic fungi into plant genomes has been proposed (Dahlman *et al.* 1991). To evaluate the environmental impacts of these advances, we will need to understand how variation among grass/endophyte genotypes affects ecological interactions within and between consumers. Because most infected tall fescue in the eastern USA hosts a single endophyte genotype found in KY-31, and because it may be highly resistant to invasion by other species or genotypes, research on genetic variation in the endophyte may be of greater academic than practical significance except in highly managed agronomic and/or turf situations.

4. Conclusions

Our conclusions are based experimental plots where fescue seed was sown on recently plowed soil that was rapidly colonized by diverse plant and animal species. No treatments, if any, were applied following seeding so long-term community and ecosystem responses are integrating the cumulative effects of many varying biotic and abiotic factors. Results from multiple experiments are highly consistent and repeatable, suggesting that we are measuring general, rather than idiosyncratic, effects of endophyte infection on communities and ecosystems.

Several general conclusions arise from this work. One is that community-level effects are much stronger than one would predict from studies on individual species. Second, more generally, our results indicate an important role for mutualism in structuring communities and suggest that mutualisms may be critical for understanding the community and ecosystem-level consequences of non-native species such as tall fescue. Third, mechanisms of community change derive from a complex mixture of direct and indirect effects (e.g., through herbivores) of the endophyte. While we have identified vole herbivory as a key indirect mechanism, the relative importance of other factors (soil feedback, allelopathy, insect herbivory, direct competition, etc.) in mediating community-level responses is unclear and represents an important area for further study. Finally, it would be very useful to study community-level effects of endophyte symbiosis in other systems to improve generalizations and predictions, e.g. in tall fescue in different ecological settings (including where it is native), in *L. perenne* in Europe, USA and New Zealand, and in other dominant native and non-native grasses worldwide.

Acknowledgements

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Appendix 1

Summary of recent studies on the effects of the tall fescue endophyte on wild animals. We included all studies published since 1996 identified by the search terms "tall fescue" and "endophyt*" and "herbivor*" (and replacing both tall fescue and endophyt* with species names) on Web of Science (with one notable exception (Muegge *et al.* 1991) because it examined a species richness response). We also included relevant data available in recent book chapters. We only included studies that experimentally manipulated endophyte presence in tall fescue and that recorded at least one fitness-related response variable to estimate animal performance. Where multiple variables were measured, an effect size was determined for each. Effect size is the log response ratio = $\ln(\text{mean}_{E-} / \text{mean}_{E+})$. Direction of the effect is for E+ relative to E- (i.e., lower means the response variable was lower in E+ relative to E-). Neutral effects (assigned an effect size of zero) were those reported as non-significant following statistical analysis. Some treatment means had to be estimated from data presented in figures, and those are indicated in the table.

Appendix 1								
Ref	Arthropod	Guild	Specialization	Direction	Effect size (L)	Response variable	Field or Lab/ Greenhouse	Means estimated from figures
(1)	<i>Chaetocnema pulicaria</i> (beetle)	leaf chewer	grass specialist	lower	0.88	percentage survival of adults after 4 d	field	
(2)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	daily food intake	lab	
(2)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	higher	-0.23	urine volume	lab	
(3)	Sminthuridae (Collembola)	detritivore	generalist	higher	n/a	number per plot	field	
(3)	<i>Lepidocyrtus cinereus</i> (Collembola)	detritivore	generalist?	lower	0.75	number per plot	field	X
(3)	<i>Homidia socia</i> (Collembola)	detritivore	generalist?	neutral	0.00	number per plot	field	
(3)	<i>Galumna</i> sp. (oribatid mite)	detritivore	generalist	lower	1.21	number per plot	field	X
(3)	<i>Epilohmannia</i> sp. (oribatid mite)	detritivore	generalist	neutral	0.00	number per plot	field	
(3)	Chloropidae (flies)	detritivore	generalist	lower	0.92	number per plot	field	X
(3)	<i>Parajapyx isabellae</i> (dipluran)	predator	generalist	neutral	0.00	number per plot	field	
(3)	Carabidae (ground beetles)	predator	generalist	neutral	0.00	number per plot	field	
(4)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	lower	0.34	larval mass	greenhouse	X
(4)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	slower	-0.04	development time	greenhouse	X
(4)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	higher	-0.16	pupal mass	greenhouse	X
(4)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	higher	-0.06	pupal mass in induced plants (pre-damaged)	greenhouse	X
(5)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	higher	-0.22	larval growth	greenhouse	
(5)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	faster	0.05	development time	greenhouse	
(5)	<i>Rhopalosiphum padi</i> (aphid)	sap feeder	grass specialist	lower	0.33	apterae density	greenhouse	
(6)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	higher	-0.18	larval mass	greenhouse	
(6)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	faster	0.04	development time	greenhouse	
(6)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	lower	0.11	pupal mass	greenhouse	
(6)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	neutral	0.00	survival	greenhouse	
(6)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	neutral	0.00	assimilation	greenhouse	
(7)	<i>Euplectrus comstockii</i> (parasitoid wasp)	parasitoid	moderate	faster	0.10	female development time	lab	X
(7)	<i>Euplectrus comstockii</i> (parasitoid wasp)	parasitoid	moderate	lower	0.41	pupal mass	lab	X
(7)	<i>Euplectrus comstockii</i> (parasitoid wasp)	parasitoid	moderate	neutral	0.00	survival	lab	
(7)	<i>Euplectrus comstockii</i> (parasitoid wasp)	parasitoid	moderate	neutral	0.00	sex ratio	lab	
(7)	<i>Euplectrus plathypenae</i> (parasitoid wasp)	parasitoid	moderate	neutral	0.00	development time	lab	
(7)	<i>Euplectrus plathypenae</i> (parasitoid wasp)	parasitoid	moderate	lower	0.37	female pupal mass	lab	X
(7)	<i>Euplectrus plathypenae</i> (parasitoid wasp)	parasitoid	moderate	neutral	0.00	survival	lab	
(7)	<i>Euplectrus plathypenae</i> (parasitoid wasp)	parasitoid	moderate	neutral	0.00	sex ratio	lab	
(8)	<i>Rhopalosiphum padi</i> (aphid)	sap feeder	grass specialist	lower	0.80	intrinsic rate of increase	greenhouse	X
(8)	<i>Rhopalosiphum padi</i> (aphid)	sap feeder	grass specialist	lower	1.56	intrinsic rate of increase following artificial clipping	greenhouse	X

(8)	<i>Rhopalosiphum padi</i> (aphid)	sap feeder	grass specialist	lower	1.10	intrinsic rate of increase (replicate experiment)	greenhouse	X
(8)	<i>Rhopalosiphum padi</i> (aphid)	sap feeder	grass specialist	lower	1.12	intrinsic rate of increase following artificial clipping (replicate experiment)	greenhouse	X
(9)	<i>Diuraphis noxia</i> (aphid)	sap feeder	grass specialist	lower	3.40	number per plant	greenhouse	X
(9)	<i>Diuraphis noxia</i> (aphid)	sap feeder	grass specialist	lower	2.52	number per plant	field	
(10)	<i>Reithrodontomys humulis</i> (mouse)	omnivore esp. seeds	generalist	lower	1.04	number caught per plot	field	
(10)	<i>Blarina brevicauda</i> (shrew)	omnivore	generalist	lower	0.66	number caught per plot	field	
(10)	<i>Microtus pinetorum</i> (vole)	root feeder	generalist	lower	0.56	number caught per plot	field	
(10)	<i>Sigmodon hispidus</i> (rat)	leaf chewer	generalist	neutral	0.00	number caught per plot	field	
(12)	<i>Microtus pennsylvanicus</i> (vole)	leaf chewer	generalist	neutral	0.00	offspring number	lab	
(12)	<i>Microtus pennsylvanicus</i> (vole)	leaf chewer	generalist	neutral	0.00	body mass	lab	
(12)	<i>Microtus pennsylvanicus</i> (vole)	leaf chewer	generalist	neutral	0.00	survival at 21C	lab	
(12)	<i>Microtus pennsylvanicus</i> (vole)	leaf chewer	generalist	lower	1.29	survival at 31C	lab	
(13)	<i>Branta canadensis</i> (Canada goose)	leaf chewer	generalist	lower	0.12	body mass	field	X
(14)	<i>Hematobia irritans</i> (fly larva)	coprophage	generalist	lower	0.94	% pupae from larvae in dung with N-formyl loline	lab	
(14)	<i>Hematobia irritans</i> (fly larva)	coprophage	generalist	lower	1.37	% pupae from larvae in dung with ergotamine tartrate	lab	
(14)	<i>Hematobia irritans</i> (fly larva)	coprophage	generalist	lower	0.10	pupal mass in dung with N-formyl loline	lab	
(14)	<i>Hematobia irritans</i> (fly larva)	coprophage	generalist	lower	0.59	pupal mass in dung with ergotamine tartrate	lab	
(14)	<i>Hematobia irritans</i> (fly larva)	coprophage	generalist	lower	0.62	% adults from larvae in dung with N-formyl loline	lab	
(14)	<i>Hematobia irritans</i> (fly larva)	coprophage	generalist	lower	1.95	% adults from larvae in dung with ergotamine tartrate	lab	
(14)	<i>Hematobia irritans</i> (fly larva)	coprophage	generalist	neutral	0.00	adult mass	lab	
(14)	<i>Hematobia irritans</i> (fly larva)	coprophage	generalist	neutral	0.00	adult mass	lab	
(15)	<i>Microtus ochrogaster</i> (vole)	leaf chewer	generalist	lower	1.44	adult male growth rate	lab	
(15)	<i>Microtus ochrogaster</i> (vole)	leaf chewer	generalist	lower	0.86	growth rate of litters	lab	
(15)	<i>Microtus ochrogaster</i> (vole)	leaf chewer	generalist	lower	1.61	number of litters produced	lab	
(15)	<i>Microtus ochrogaster</i> (vole)	leaf chewer	generalist	lower	1.63	percentage of offspring surviving to 21 d	lab	
(16)	<i>Meloidogyne marylandi</i> (root knot nematode)	root endoparasite	grass specialist?	lower	3.98	number of nematodes per pot	greenhouse	
(17)	rabbit (species name not given)	leaf chewer	generalist	lower	0.73	male body mass	lab	
(18)	Araneae (spiders)	predator	generalist	neutral	0.00	total abundance		
(18)	Araneae (spiders)	predator	generalist	lower	0.13	morphospecies richness		
(18)	Araneae (spiders)	predator	generalist	lower	0.16	family richness		
(18)	Linyphidae (sheet web spiders)	predator	generalist	lower	0.63	number per subplot		
(18)	Thomisidae (crab spiders)	predator	generalist	lower	0.85	number per subplot		
(18)	Salticidae (jumping spiders)	predator	generalist	higher	-0.66	number per subplot		
(19)	<i>Microtus ochrogaster</i> (vole)	leaf chewer	generalist	neutral	0.00	number per plot	field	

(continued on next page)

Appendix 1 (continued)								
Ref	Arthropod	Guild	Specialization	Direction	Effect size (L)	Response variable	Field or Lab/ Greenhouse	Means estimated from figures
(19)	<i>Microtus ochrogaster</i> (vole)	leaf chewer	generalist	higher	-0.32	proportion of males (skewed sex ratio)	field	
(19)	<i>Microtus ochrogaster</i> (vole)	leaf chewer	generalist	neutral	0.00	rate of sexual maturity in males	field	
(19)	<i>Microtus ochrogaster</i> (vole)	leaf chewer	generalist	lower	1.24	rate of sexual maturity in females	field	X
(19)	<i>Microtus ochrogaster</i> (vole)	leaf chewer	generalist	neutral	0.00	growth rate of individuals	field	
(20)	<i>Microtus ochrogaster</i> (vole)	leaf chewer	generalist	neutral	0.00	home range size	field	
(21)	<i>Eisenia fetida</i> (earthworm)	detritivore	generalist	neutral	0.00	survival	lab	
(21)	<i>Eisenia fetida</i> (earthworm)	detritivore	generalist	greater	-1.30	growth	lab	
(21)	<i>Eisenia fetida</i> (earthworm)	detritivore	generalist	lower	0.29	reproduction	lab	
(22)	<i>Rhopalosiphum padi</i> (aphid)	sap feeder	grass specialist	lower	1.28	intrinsic rate of increase (clip cage)	greenhouse	X
(22)	<i>Rhopalosiphum padi</i> (aphid)	sap feeder	grass specialist	lower	2.54	intrinsic rate of increase (enclosure)	greenhouse	X
(23)	<i>Parapediasia teterrella</i> (webworm)	leaf chewer	grass specialist	lower	4.44	survival		
(24)	<i>Exomala orientalis</i> (beetle)	root feeder	generalist	higher	1.03	susceptibility to nematode	greenhouse	
(24)	<i>Popilla japonica</i> (Japanese beetle)	root feeder	generalist	neutral	0.00	susceptibility to nematode	greenhouse	
(24)	<i>Cyclocephala borealis</i> (beetle)	root feeder	generalist	neutral	0.00	susceptibility to nematode	greenhouse	
(24)	<i>Exomala orientalis</i> (beetle)	root feeder	generalist	neutral	0.00	susceptibility to nematode	field	
(24)	<i>Popilla japonica</i> (Japanese beetle)	root feeder	generalist	neutral	0.00	susceptibility to nematode	field	
(24)	<i>Cyclocephala borealis</i> (beetle)	root feeder	generalist	neutral	0.00	susceptibility to nematode	field	
(24)	Formicidae (ants)	predator	generalist	neutral	0.00	number per plot	field	
(24)	Araneae (spiders)	predator	generalist	neutral	0.00	number per plot	field	
(24)	Staphylinidae (beetles)	predator	generalist	neutral	0.00	number per plot	field	
(24)	Carabidae (ground beetles)	predator	generalist	neutral	0.00	number per plot	field	
(24)	<i>Exomala orientalis</i> (beetle)	root feeder	generalist	lower	0.63	survival	greenhouse	
(24)	<i>Exomala orientalis</i> (beetle)	root feeder	generalist	neutral	0.00	body mass	greenhouse	
(24)	<i>Popilla japonica</i> (Japanese beetle)	root feeder	generalist	neutral	0.00	survival	greenhouse	
(24)	<i>Popilla japonica</i> (Japanese beetle)	root feeder	generalist	neutral	0.00	body mass	greenhouse	
(24)	<i>Exomala orientalis</i> (beetle)	root feeder	generalist	lower	0.76	survival	field	
(24)	<i>Exomala orientalis</i> (beetle)	root feeder	generalist	neutral	0.00	body mass	field	
(24)	<i>Popilla japonica</i> (Japanese beetle)	root feeder	generalist	neutral	0.00	survival	field	
(24)	<i>Popilla japonica</i> (Japanese beetle)	root feeder	generalist	lower	0.19	body mass	field	
(24)	white grubs (all species, Scarabidae)	root feeder	generalist	higher	-0.56	number per plot (avg of several censuses)	field	
(25)	Collembola	detritivore	generalist	neutral	0.00	number per plot		
(25)	Hypogastruridae (collembola)	detritivore	generalist	higher	-0.52	number per plot		
(25)	Isotomidae (collembola)	detritivore	generalist	lower	0.36	number per plot		
(26)	<i>Spodoptera frugiperda</i> (caterpillar)	leaf chewer	generalist	lower	0.36	relative growth rate	greenhouse	
(27)	<i>Schistocerca gregaria</i> (locust)	leaf chewer	generalist	neutral	0.00	survival	field	
(28)	<i>Agallia constricta</i> (leafhopper)	sap feeder	grass specialist	lower	0.73	number per plot	field	X
(28)	<i>Agallia deleta</i> (leafhopper)	sap feeder	grass specialist	neutral	0.00	number per plot	field	X

(28)	<i>Draeculacephala</i> spp. (leafhopper)	sap feeder	generalist	lower	1.06	number per plot	field	X
(28)	<i>Exitianus exitiosus</i> (leafhopper)	sap feeder	grass specialist	lower	1.43	number per plot	field	X
(28)	<i>Graminella nigrifrons</i> (leafhopper)	sap feeder		lower	1.67	number per plot	field	X
(28)	<i>Unerus colonus</i> (leafhopper)	sap feeder		neutral	0.00	number per plot	field	X
(28)	<i>Prosapia bicincta</i> (froghopper)	sap feeder	grass specialist	lower	1.59	number per plot	field	X
(28)	species diversity (cicadellidae and cercopidae)	sap feeder		lower	0.26	species diversity (index not given)	field	X
(29)	<i>Rhopalosiphum padi</i> (aphid)	sap feeder	grass specialist	neutral	0.00	number of apterae per plant	greenhouse	
(30)	<i>Balannococcus poae</i> (mealybug)	sap feeder	grass specialist	lower	2.41	percentage infestation		
(31)	<i>Popilla japonica</i> (Japanese beetle)	root feeder	generalist	neutral	0.00	body mass	greenhouse	
(31)	<i>Popilla japonica</i> (Japanese beetle)	root feeder	generalist	neutral	0.00	survival	greenhouse	
(32)	<i>Phenacoccus solani</i> (mealybug)	sap feeder	grass specialist	lower	4.19	number per plant	greenhouse	
(32)	<i>Phenacoccus solani</i> (mealybug)	sap feeder	grass specialist	lower	3.43	number per plant	greenhouse	
(32)	<i>Sipha maydis</i> (aphid)	sap feeder	grass specialist	lower	0.84	number per plant	greenhouse	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	body mass - male	lab - 62 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	body mass - female	lab - 62 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	reproductive organ mass - male	lab - 62 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	reproductive organ mass - female	lab - 62 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	body mass - male	lab - 113 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	body mass - female	lab - 113 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	reproductive organ mass - male	lab - 113 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	reproductive organ mass - female	lab - 113 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	mean number of litters per female	lab - 113 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	number of offspring per litter	lab - 113 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	body mass -unpaired female	lab - 113 d	
(33)	<i>Peromyscus leucopus</i> (mouse)	seed predator	generalist	neutral	0.00	reproductive organ mass - unpaired female	lab - 113 d	
(34)	<i>Acromyrmex versicolor</i> (ant)	leaf chewer	generalist	lower	0.97	queen survival time	lab	X
(34)	<i>Acromyrmex versicolor</i> (ant)	leaf chewer	generalist	lower	13.16	queen percentage survival after 11 wks	lab	
(34)	<i>Acromyrmex versicolor</i> (ant)	leaf chewer	generalist	neutral	0.00	worker number	lab	
(34)	<i>Acromyrmex versicolor</i> (ant)	leaf chewer	generalist	lower	12.15	fungal garden size	lab	
(35)	<i>Agrotis ipsilon</i> (black cutworm)	leaf chewer	generalist	neutral	0.00	larval mass	greenhouse	
(35)	<i>Agrotis ipsilon</i> (black cutworm)	leaf chewer	generalist	neutral	0.00	pupal mass	greenhouse	
(35)	<i>Agrotis ipsilon</i> (black cutworm)	leaf chewer	generalist	neutral	0.00	days to emergence	greenhouse	
(35)	<i>Agrotis ipsilon</i> (black cutworm)	leaf chewer	generalist	neutral	0.00	percentage survival	greenhouse	
	average				0.66			
	vertebrate herbivores				0.31			
	leaf chewers				0.54			
	seed predators				0.05			
	invertebrate herbivores				1.01			
	sap feeders				1.47			
	leaf chewers				1.59			

(continued on next page)

Appendix 1 (continued)								
Ref	Arthropod	Guild	Specialization	Direction	Effect size (L)	Response variable	Field or Lab/ Greenhouse	Means estimated from figures
	root feeders				0.33			
	generalist				0.74			
	grass specialist				1.84			
	non-herbivores				0.24			
	detritivores				0.15			
	predators/parasitoids				0.10			
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